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Multiple pathways mediate the effects of climate change on maternal reproductive traits in a red deer population

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Abstract. Temporal changes in phenological traits arising as a consequence of recent rapid environmental change have been widely demonstrated in animal populations. Increasingly, studies are seeking to understand the impact of changes in such traits on individual fitness and population dynamics, with the ultimate aim of predicting population persistence or extinction under different climate scenarios. Here, we examined the effects of environmental change on maternal reproductive traits in a wild population of red deer (*Cervus elaphus*) and sought to explain why, despite a rapid advance in offspring birth dates, we observed no apparent consequences for offspring fitness. By using path analysis, we identified both direct and indirect paths along which changes in environmental conditions affected birth date, birth mass, juvenile survival, and female fecundity. In general, warmer temperatures were associated with earlier birth dates and greater birth mass, and higher rainfall was associated with reduced juvenile survival and reduced female fecundity. We also examined concurrent effects of population density, maternal age, and reproductive history, and found that temporal stasis in average trait values, at least in part, could be explained by antagonistic roles of direct and indirect effects of changing climate and increasing population density. Identification of the many mechanisms that contribute to the dynamics of phenotypic traits is challenging; this study demonstrates the need to consider both climatic and demographic variation in order to understand the fitness consequences of changes in phenological traits.

Key words: Cervus elaphus; *climate change; demography; fitness; Isle of Rum, Scotland; maternal traits; path analysis; phenology; red deer; reproduction.*

Introduction

Changes to the earth's climate, predominantly attributable to anthropogenic change, have been widely shown to be occurring at an unprecedented rate (Karl and Trenberth 2003, Solomon et al. 2007), with the greatest changes occurring in northern latitudes (Dickinson 1986). A large number of studies have now demonstrated changes in phenological traits in plant and animal populations associated with this environmental change (Parmesan 2006, Thackeray et al. 2010). However, we still have only limited understanding both of the mechanisms underlying such changes in phenology and, crucially, of their fitness consequences for individuals and populations (Visser and Both 2005, Visser 2008, Ozgul et al. 2010, Lane et al. 2012, van de Pol et al. 2012, Gienapp et al. 2013, Reed et al. 2013). An understanding of both of these aspects is valuable for disentangling the roles of phenotypic plasticity, demography, and microevolution in explaining trait dynamics under climate change, and ultimately, for predicting the consequences of climate change for population persistence or extinction (Chevin et al. 2010, Cahill et al. 2013, Moritz and Agudo 2013).

For animals, there are several challenges in predicting the consequences of changing environment for individual fitness and, hence, population dynamics, particularly in strongly seasonal environments. Firstly, there may be a delay between the timing of the environmental cue influencing the trait value and the point at which the trait is expressed, and hence at which selection acts (Visser et al. 2004). Secondly, effects of phenological change on fitness may depend on the extent to which rates of phenological response are matched across trophic levels (e.g., predator and prey or herbivore and plant abundance). For example, both caribou (*Rangifer tarandus*) and Great Tits (*Parus major*) have been shown to have reduced fitness as a result of a mismatch between the rate of advance of calving or laying dates and the rate of advance in the peak of food availability (Visser et

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al. 1998, Post and Forchhammer 2008), However, it should be noted that in the case of Great Tits, although females with high levels of individual mismatch recruited fewer offspring, across years the relationship between annual average measures of fitness and population-level mismatch was weak or absent (Reed et al. 2013). Finally, the effects of climate change on fitness may vary within species, particularly if there is variation in the extent to which individuals are plastic in their response to changing environmental cues (Visser et al. 2003, Visser et al. 2004, Charmantier et al. 2008, Husby et al. 2010).

Currently, the majority of phenological responses to climate change have been documented in birds (Berteaux and Stenseth 2006, Parmesan 2006, Thackeray et al. 2010), although an increasing number of studies have found evidence of phenological changes in mammal populations (Réale et al. 2003, Berteaux and Stenseth 2006, Post and Forchhammer 2008, Ozgul et al. 2010, Burthe et al. 2011, Moyes et al. 2011, Lane et al. 2012). Unlike birds, in temperate environments, ungulates and other long-lived mammals typically have a long, overwinter gestation period, so there may be a substantial lag between the environmental cues determining the timing of important phenological events and the point at which the event actually occurs. Trends in climate may vary in their strength or direction between months or seasons; for example, summer rainfall may increase while winter rainfall remains unchanged. Further, weather may be related to the trait in a variety of ways. For example, warmer temperatures have been associated with both increased and decreased body size in northern ungulate populations, depending on the time of year considered (Post and Stenseth 1999, Weladji and Holand 2003). Therefore identifying the critical time windows during which different environmental cues affect trait expression is crucial for understanding phenological changes (van de Pol and Cockburn 2011). Herbivores are likely to be both directly influenced by climatic conditions through energy demands and indirectly influenced through plant productivity (Sæther 1997, Stenseth et al. 2002, Forchhammer and Post 2004). Therefore, the multiple pathways via which the environment influences herbivore ecology potentially can make it challenging to identify drivers of environmental change (Mysterud et al. 2008, Martinez-Jauregui et al. 2009). Further, observed changes in phenotypic traits need to be considered in the context of changes in population demography such as population density and age structure (whether occurring independently or as a direct or trait-mediated effect of environmental change), because these can potentially reinforce or dampen climatic effects on traits (Torres-Porras et al. 2009, Ozgul et al. 2010, van de Pol et al. 2012).

In this study, we examined the associations between weather, demography, and a set of traits associated with female reproduction (parturition date or "birth date" of offspring, offspring birth mass, offspring first-year survival, and female fecundity), in a wild population of red deer (*Cervus elaphus*) on the Isle of Rum, off the west coast of Scotland. The red deer is a large, polygynous herbivore with a wide distribution across regions experiencing temperate climates. In Scotland, red deer are an asset to the economy due to hunting, food, and recreational opportunities, but they also generate costs due to the need to manage populations to protect woodlands and certain plant communities in the absence of natural predators (Scottish Natural Heritage 2010). Therefore, understanding how the fitness of red deer may change in response to ongoing climate change will be important for determining future management regimes. Here, we use data from a long-term, individual-based study of red deer on the Isle of Rum, Scotland (Clutton-Brock et al. 1982).

A previous analysis (Moyes et al. 2011) of data from the long-term study of red deer on the Isle of Rum documented significant temporal advances in a number of phenological traits, including mean parturition date, across the period 1980–2007. Moyes et al. (2011) considered how one temperature-based, environmental measure ("growing degree-days," GDD) might influence trends in phenology, but did not consider demographic influences. As such, although the analysis demonstrated conclusively that birth dates had advanced over the last three decades, it did not explore how environmental or demographic changes might drive this pattern. Further, although previous work on the study population has shown direct links between a calf's birth date, its birth mass, and its subsequent early survival (Clutton-Brock et al. 1982, Coulson et al. 2003), surprisingly, there was no indication of a trend in average birth mass or juvenile survival in accordance with the trend of advancing birth date (Moyes et al. 2011). In the present study, we used a longer time series (1971–2009) and a broader assessment of the influence of multiple local climatic factors as well as demographic variables on patterns of variation in parturition dates. We also aimed to explain the apparent paradox of stasis in offspring birth mass and juvenile survival by identifying the multiple pathways by which both climate and population density may affect these traits. Further, we examined the effects of climate and population density on female fecundity: although Moyes et al. (2011) did not consider fecundity, previous studies have shown this to be a highly plastic reproductive trait that is associated with both weather and population density (Kruuk et al. 1999, Coulson et al. 2000).

Our aim was therefore to identify the critical periods of the year during which climate affects expression of four maternal reproductive traits: offspring birth date, offspring birth mass, offspring juvenile survival, and female adult fecundity. From earlier work on this population, we can identify a priori expectations as to which aspects of climate at particular times of year are likely to affect the different traits. In particular, increased rainfall in late autumn should delay offspring birth date (Nussey et al. 2005*b*), warmer temperatures in late spring should increase birth mass (Albon et al. 1983,

Nussey et al. 2005*a*), and higher rainfall through the winter should decrease both juvenile survival and female fecundity (Coulson et al. 1999, Kruuk et al. 1999, Post and Stenseth 1999, Walling et al. 2011). However, these previous analyses concerned only single weather variables affecting single traits at a time, and did not include data from the most recent (and hence warmest and wettest; Barnett et al. 2006) decade. We therefore undertook a detailed analysis of the effects of multiple aspects of local climate (minimum and maximum daily temperature, precipitation, and wind speed), comparing time windows of varying length across the year. To ensure a fully objective assessment of potential effects, we considered windows of all possible combinations of start date and duration in weeks leading up to each trait. We then used confirmatory path analysis to test whether these weather variables explained observed temporal change or stasis in each phenotypic trait, when considered within a framework that also accounted for phenotypic correlations between traits, population size, and maternal characteristics (age and reproductive status). Unlike regression analyses, which can only test the dependence of response variables on a set of predictor variables, path analysis can test the structural nature of multiple relationships between different variables, allowing us to identify both direct and indirect (acting via other variables) effects on the trait in question (Thomas et al. 2007, Shipley 2009).

Materials and Methods

Data

We used 39 years of data (1971–2009) recorded in a wild population of red deer living in the North Block of the Isle of Rum, Scotland (57°01′ N, 6°17′ W). This unmanaged population has been intensively monitored since the early 1970s, and all individuals can be recognized by artificial or natural markings (Clutton-Brock et al. 1982). In 1973, culling in the population ceased, following which there was a sharp increase in population size (Coulson et al. 2004). Piecewise regression models suggest that this sharp increase persisted until 1980 at a rate of 14.1 ± 1.2 additional females (≥1 year old; mean ± SE) per year; since 1980 the population has been increasing at a lower, but still significant, rate (1.1 ± 0.3 additional females per year, $P < 0.001$; see Appendix Fig. A1a). In 2011, the population size was 178 adult females.

The annual breeding cycle of red deer consists of an autumn rut, during which males compete to defend harems of females and to mate with females in those harems who come into estrus. In our study population, this rutting period occurs from mid-September to mid-November, although female estruses are relatively synchronized, with an approximately two-week peak of conceptions in mid-October. Female estrus lasts at most 24 hours, but a female that does not become pregnant in a given estrus may come into estrus a second time ~18 days later (Guinness et al. 1971). Female gestation length is ~236.5 days, and is relatively, although not entirely, invariant (±6.2 SD; Clements et al. 2011). Females therefore give birth to calves during May and June, and lactation continues until at least the following autumn, when they may conceive again. In this population, females do not calve before the age of three, and give birth to at most one offspring per year. Average longevity of females that survive to breeding age is 11 years, so our data contain many repeated observations on the same individual; however, the vast majority of females do not calve in every year of life (average female fecundity each year is 63%).

Regular censuses and mortality searches are undertaken throughout the year to measure population size and to assess mortality for all individuals (Clutton-Brock et al. 1982). Mark–recapture analyses show that annual "recapture" (essentially resighting) probabilities for individuals are effectively 1.0 (Catchpole et al. 2004). In addition, during the calving season, all females are assessed visually to determine whether they are pregnant, and daily observations are made to record the date of birth for all calves born. The majority of calves (70% of those with known birth date) are caught shortly after birth, when they are given individually recognizable tags, sexed, and weighed (Clutton-Brock et al. 1982); maternity is then confirmed from subsequent field observations of females and their calves. The peak period of mortality occurs during February–April, which is when 67% of deaths due to natural mortality occur (natural mortality is predominantly due to starvation). Years are defined as "deer years," where "deer year t" runs from 1 May in year t to 30 April in year $t + 1$.

Reproductive traits and other measures

We considered the following maternal reproductive traits:

1) *Birth date*, the date on which a calf was born, in days of the year (1 Jan = 1; $N = 3169$ records from 693 mothers).
2) *Birth mass*, the body mass at calf capture, adjusted for time since birth to give an estimated birth mass in kilograms (birth mass = capture mass − [0.01539 × age at capture in hours], following Clutton-Brock et al. (1982); $N = 2298$ records from 602 mothers).
3) *Juvenile survival*, determined as whether or not a calf survived until 1 May of the year following its birth, excluding any individuals that were shot when venturing outside the study area ($N = 3016$ records from 668 mothers).
4) *Fecundity*, determined as whether or not an adult female (≥3 years old in the year of calving) gave birth in a given year, estimated for all years of an adult female's life in which she was known to be resident in the study population from census records (specifically, seen in at least 10% of censuses, following Coulson et al. [2004]). Records for

fecundity are only available since 1974, when regular censusing begun; for this data set, we can only consider 36 years of fecundity data ($N = 4937$ records on 574 females).

The following variables were included in models:

1) *Reproductive status*, determined as whether or not a female still had a live calf from the previous year at the time of calving; females are classed as "milk" (live calf) vs. "yeld," with first-time mothers grouped in the yeld category. Previous work has shown that current female performance is associated with reproductive status (Clutton-Brock et al. 1982, Coulson et al. 2003).
2) *Population size (or density)*, the number of females $\geq$1 year old that are defined as resident (specifically, seen in at least 10% of censuses) in the population, assessed using census data during the period January to May (Coulson et al. 2004).
3) *Year* (deer year, as previously defined), included as a continuous variable in models to test for temporal trends.
4) *Female age*, in years, fitted with a quadratic term to account for reproductive senescence (Nussey et al. 2009), and defined as the age she would reach in that deer year (e.g., a female born in June 2006 giving birth to a calf in May 2010 was classified as a four-year-old).
5) *Sex of offspring or of previous offspring*; sex of offspring was fitted in the model of offspring birth date, birth mass, and juvenile survival. Sex of a female's previous offspring (if applicable) was fitted in the fecundity model; where the latter was unknown, it was treated as missing data.

Weather data

Many studies of environmental effects on ungulate populations have focused on broadscale measures of climate, such as the North Atlantic Oscillation Index, to explain observed variation in phenotypes (Forchhammer et al. 1998, Post and Stenseth 1999, Ottersen et al. 2001, Stenseth et al. 2002). However, local weather variables may be more suitable candidates for drivers of variation, not least because it is generally easier to interpret the mechanisms underlying their effects, and because these effects are not complicated by varying associations between local conditions and large-scale indices (e.g., see discussions in Pettorelli et al. 2006, Martinez-Jauregui et al. 2009, van de Pol et al. 2013). Previously, the effects of climate change on the Rum study population have been examined using "growing degree-days" (GDD), the cumulative sum of the daily mean temperatures above a threshold during a given period, as a measure of climate, assuming a relevant temperature threshold for GDD of 5°C (Moyes et al. 2011). Here we used raw weather data, rather than GDD because we wanted to consider other climatic measures: both maximum and minimum temperature, as well as precipitation and wind speed; further, it has been shown in other systems that findings based on using temperature in a time-window approach gives congruent results with a GDD model (Phillimore et al. 2013); for further discussion regarding choice of weather variables, see the Appendix.

We used a time series of daily weather from 1970 to 2009 (i.e., starting in the year preceding the first deer records used here) for four weather variables: maximum temperature (°C), minimum temperature (°C), total precipitation (mm, hereafter termed rainfall), and average wind speed (m/s). With the exception of wind speed, this time series was a composite of local automatic weather station (AWS) data (1971–1999) and daily spatially interpolated data for the periods when the AWS was not available (1970, and 2000 onward). The interpolated data were reconstructed using proxies from both Tiree weather station data (available at the British Atmospheric Data Centre, BADC) and gridded data (Met Office United Kingdom Climate projections, UKCP09). The reconstructed daily weather time series was interpolated using equations resulting from generalized additive models' calibration for months for the period 1971–1999. The wind speed data used throughout were collected from the Tiree weather station (BADC). Annual values of the four weather variables are shown in Appendix Fig. A1.b; for further details on the weather data, see Bento (2012).

Statistical analyses

All analyses were conducted in R version 2.13.2 using either the "stats" or "lme4" packages (R Development Core Team 2011).

Identification of critical time window of climatic variation.—To find the key weather variables determining trait expression, we used associative modeling, specifically a sliding-window approach (Estrella et al. 2007, Brommer et al. 2008, Husby et al. 2010). In this approach, the mean of a particular weather variable (or, in the case of rainfall, the sum) is calculated across a given time period (window) and then tested for the strength of association with the trait of interest. These tests were done within a linear model framework with no other fixed effects included. The start date and duration (width) of the window was then varied, and the consequent strength of associations with the trait was recalculated in order to identify the critical time window that had the greatest association with trait expression (van de Pol and Cockburn 2011).

To identify the critical window of each weather variable with most statistical support, we compared the Akaike information criterion (AIC) values of linear models containing windows varying by weekly intervals in start date and duration, with the longest possible interval being 52 weeks. Each linear model contained only one potential window. All potential windows were considered in either the "deer year" (1 May to 30 April) preceding calving (for analyses of birth date, mass, and

fecundity) or the deer year following calving (juvenile survival). We chose the critical window from the model with the lowest AIC as most informative. For each trait, once we had identified the best critical window for each weather variable, we assessed which combination of the four weather variables had the highest statistical support when considered in the same model (a total of 15 possible models for all possible combinations of the four variables). Again, we used AIC for model comparison. We also estimated AIC weights, defined as:

$$\mathrm{AIC_{wt}} = \exp(-\Delta\mathrm{AIC}/2)/\sum \exp(-\Delta\mathrm{AIC}/2)$$

where the sum is across all 15 models for that trait, and ΔAIC represents the difference in AIC between that model and the best (i.e., lowest AIC) model; this indicates the relative support for the best model. We then used the combination associated with the lowest AIC values in the path analyses.

Path analyses

We used confirmatory path analysis in order to test the effects of weather, population density, maternal characteristics (age and reproductive status (milk or yeld, as defined previously)), and also, where relevant, the other reproductive traits on birth date, birth mass, juvenile survival, and female fecundity. To test the causal implications of our hypothesized path models, we used Shipley's method, based on the concept of "d-separation" (directed separation; Verma 1988, Geiger et al. 1990, Shipley 2000*b*). D-separation is defined as the necessary and sufficient conditions for two vertices in a directed acyclic (i.e., without feedback) graph (such as the typical box and arrow diagram used in path analysis) to be independent upon conditioning on another set of vertices (Shipley 2000*a*).

In this method, conditional independence of variables within the model is taken to be a description of the statistical patterns of conditional dependence and independence that would be true in the observed data if they were generated by the hypothesized causal process. For example, conditional independence of two variables, X and Y, given variables Z_1 and Z_2, is tested by obtaining the null probability that the slope of X is zero in a linear model with structure $Y \sim Z_1 + Z_2 + X$. A test of the causal hypothesis represented by the causal graph is therefore performed by a simultaneous test of all such independence claims in that causal graph. This set of independence claims is described as a "basis set"; it consists of each pair of variables in the graph that are not directly linked by an arrow (e.g., X and Y) and the conditioning set Z for each pair that contains all variables that are direct causes of either X and Y (in the example here, Z_1 and Z_2). Therefore the basis set implies all of the claims of dependence and independence made by the causal graph. The full set of k independence claims in the basis set, with null probabilities (p_i) generated by the model, is tested simultaneously to give the statistic $C = -2\sum \ln(p_i)$. Because the null probabilities of each independence claim are mutually independent, C follows a chi-square distribution with $2k$ degrees of freedom. Lack of significant ($P < 0.05$) difference between the observed and predicted pattern of independencies in the basis set implies that the cause-order effects hypothesized in the path model are correct and therefore the model is supported (Thomas et al. 2007, Shipley 2009). The approach is easily extended to data with a hierarchical structure such as here (repeated measurements made on the same individuals), by using generalized mixed models to obtain the null probability (p_i) for each independence claim (known as generalized multilevel path models; Shipley 2009).

Here we present two path models: a "birth traits model," in which we examined variables affecting birth date, birth mass, and juvenile survival, and a "fecundity model," in which we examined effects on adult female fecundity. In addition to weather, year, and population size, models of all four traits contained the mother's age (quadratic) and reproductive status. Models of the three birth traits also contained the sex of the offspring, whereas the model of fecundity also contained the sex of the previous offspring.

The causal relationships tested in both models were hypothesized based on the following points:

1) The identified critical windows of weather were expected to have direct effects on the relevant trait.
2) Relationships between maternal characteristics and traits were hypothesized from previous studies, e.g., effects of maternal age and reproductive status on birth mass (Coulson et al. 2003, Nussey et al. 2009), and associations between birth date and birth mass (Coulson et al. 2003).
3) Hypothesized correlations among the weather variables and population size were deduced from correlation matrices used for exploratory analysis (for example, between maximum temperature in year_t and in year_{t+1}). A correlation was hypothesized if the estimated correlation coefficient given in the matrix was at least twice as large as its associated standard error.
4) Finally, a hypothesized relationship between maximum temperature and female age was proposed in the fecundity model, given that a significant correlation was indicated by exploratory analyses.

The conditional independence of pairs of variables was tested in linear (lm), linear mixed (lmm), and generalized linear mixed (glmm) models, with random effects and error structures appropriate to the respective pair of variables. To estimate relationships between annual variables, such as population size and climate, linear models were used. For all maternal traits, for which each female had multiple records (i.e., birth traits, fecundity, age, reproductive status, and offspring sex), lmms or glmms were used, with female identity fitted as a random effect. Year was also fitted as a multilevel random effect, to account for stochastic variation

TABLE 1. The highest-ranking five models testing the effect of weather variables only on birth date, birth mass, juvenile survival, and fecundity in red deer (*Cervus elaphus*) on the Isle of Rum, Scotland.

Variables	*K*	AIC	ΔAIC	AIC_{wt}
Birth date				
Max. temp. + Min. temp. + Wind speed	3	25 759.92	0.00	0.524
All four weather variables	4	25 760.20	0.28	0.455
Max. temp. + Min. temp.	2	25 768.93	9.01	0.006
Max. temp. + Rainfall	2	25 769.19	9.27	0.005
Min. temp. + Rainfall	2	25 769.46	9.54	0.004
Birth mass				
Max. temp.	1	6 980.12	0.00	0.435
Max. temp. + Wind speed	2	6 981.36	1.24	0.234
Max. temp. + Rainfall + Wind speed	3	6 983.01	2.89	0.103
Max. temp. + Rainfall	2	6 983.28	3.16	0.090
Max. temp. + Min. temp.	2	6 985.37	5.25	0.032
Juvenile survival				
Max. temp. + Min. temp. + Rainfall	3	3 617.95	0.00	0.578
All four weather variables	4	3 619.89	1.94	0.219
Max. temp. + Rainfall	2	3 621.37	3.42	0.104
Max. temp. + Rainfall + Wind speed	3	3 623.26	5.31	0.041
Min. temp. + Rainfall	2	3 623.37	5.42	0.039
Fecundity				
Max. temp. + Rainfall	2	6 231.60	0.00	0.354
Max. temp. + Min. temp. + Rainfall	3	6 232.60	1.00	0.215
Max. temp. + Rainfall + Wind speed	3	6 232.75	1.15	0.199
All four weather variables	4	6 233.66	2.06	0.126
Rainfall	1	6 236.59	4.99	0.029

Notes: Models are ordered by AIC, i.e., with the best model first. For each trait, the five models with lowest AIC are shown; details of all models fitted for each trait (a total of 15 models per trait) are in Appendix Table A1. Here, *K* is the number of weather parameters fitted; ΔAIC is the difference from the AIC of the best model. AIC weights (defined in *Methods*) give the weight of the model relative to all 15 models fitted for that trait (i.e., all models as shown in Table A1; values for the five models shown here therefore do not sum to 1). See *Results* for the dates defining the critical period for each weather variable.

between years (rather than to test for a directional temporal trend, which was tested for by fitting year as a fixed effect). All models were fitted assuming Gaussian errors, with the exception of female fecundity and juvenile survival, which were fitted as glmms with binomial error structures and logit link function.

Following identification of the appropriate model, the same statistical methods were used to test the association between pairs of variables hypothesized to be related, i.e., to test conditional *dependence* of pairs of variables. Where such associations were significant, partial regression coefficients for each significant path (hereafter termed path coefficients, β) were calculated with their standard errors. All numeric variables in the path model were standardized to mean of 0 and variance of 1 prior to calculation of path coefficients; as with hypothesis testing, coefficients were calculated in mixed-effect models with appropriate random effects where necessary.

Estimating temporal trends predicted by the path analysis models

To calculate the temporal change in birth traits and fecundity predicted by our models, the outcome of each path linking year to trait, usually via other variables and involving a total of *i* path coefficients, was calculated as $\beta_1 \times \beta_2 \times \beta_3 \times \beta_i$. The sum of all such paths was then calculated to give an overall effect of year on trait. To incorporate the error around each estimated path coefficient, we generated a distribution of each estimated coefficient, β_j, given the estimate value and standard error (assuming a normal distribution of the coefficient). The predicted change in the trait over time was then estimated 1000 times, taking independent samples from the appropriate path coefficient distributions. This gave 1000 values of the predicted temporal change for each of the birth traits and fecundity variables.

We then compared the predicted temporal changes in each trait with the magnitude of the observed temporal change, assessed using a mixed-effects model with year only as a fixed effect (continuous variable), and year and mother's identity as multilevel random effects. Both the trait and year values were standardized in this model to enable comparison with the path model prediction; however, unstandardized values of the observed change are also presented.

RESULTS

Critical windows of weather

The critical windows of mean weather (maximum temperature, minimum temperature, rainfall, and wind speed) that best explained variation in each of birth date, birth mass, juvenile survival, and fecundity were deduced from the AIC comparisons of models containing different combinations of weather variables for each trait. The best five models for each trait are given in Table 1, and the dates for the respective windows are

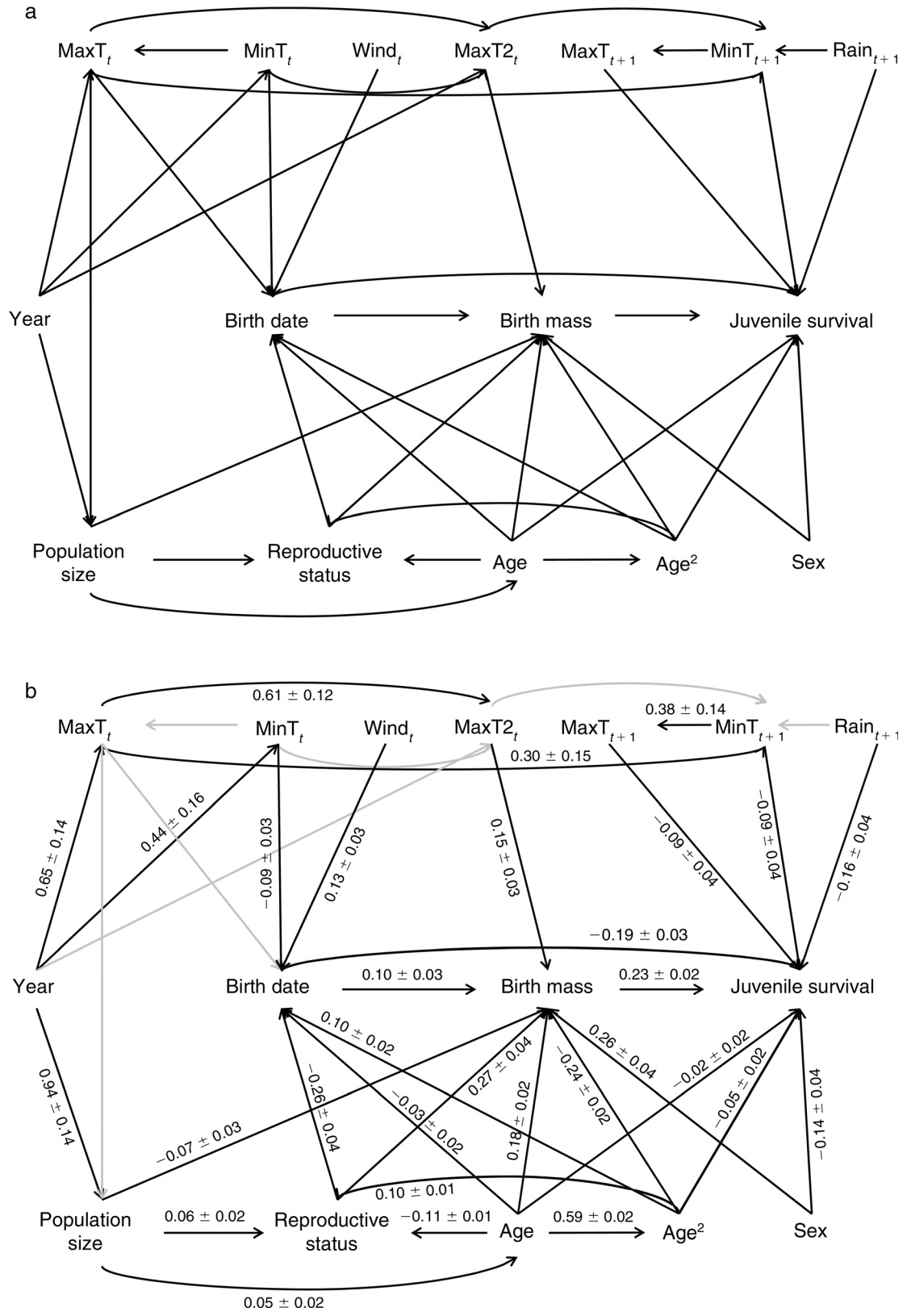

FIG. 1. (a) Hypothesized birth traits path model for red deer (*Cervus elaphus*) on the Isle of Rum, Scotland. See *Methods* for definitions of weather variables and explanation of hypothesized relationships. (b) Birth traits path model with standardized coefficients (β) and SEs given for paths associated with statistically significant effects. For reproductive status, the effect shown is of

presented in this section. In the Appendix, Figs. A2–A5 show the AIC values for the different sliding windows for each trait, and Appendix Table A1 shows details of the models of all combinations of the best windows for each weather variable.

Model selection indicated that for birth date, the best model included mean maximum temperature between 17 July and 16 April ("$MaxT_t$"), mean minimum temperature between 1 May and 21 August ("$MinT_t$"), and mean wind speed between 4 September and 18 September ("$Wind_t$") in the year preceding birth (Table 1; Appendix Fig. A2). However, a second model which additionally incorporated rainfall between 5 June and 4 December had nearly as high support ($\Delta AIC = 0.28$; AIC_{wt} of 0.52 vs. 0.46 for the two models, respectively; Table 1).

For birth mass, the best model contained only maximum temperature in the 10 weeks prior to birth, between 19 February and 30 April ("$MaxT2_t$"; Table 1; Appendix: Fig. A3).

For juvenile survival, the best model contained maximum temperature between 8 May and 10 July ("$MaxT_{t+1}$"), minimum temp between 8 May and 29 May ("$MinT_{t+1}$"), and rainfall between 10 July and 12 February in the year following birth ("$Rain_{t+1}$"; Table 1; Appendix: Fig. A4).

Finally, for fecundity, the best model contained mean maximum temperature between 25 September and 2 October and mean rainfall between 11 September and 18 September, i.e., immediately before the preceding rut (Table 1; Appendix: Fig. A5).

Path analysis

The structure of the hypothesized path models is shown for the birth traits model in Fig. 1a and for the fecundity model in Fig. 2a. Figs. 1b and 2b then show the path models characterized by the path coefficients for all significant paths, with nonsignificant paths removed.

The structure of the path model for birth traits provided a good fit to the observed data, as indicated by a nonsignificant P value of the goodness-of-fit test ($\chi^2 = 173.5$, $df = 168$, $P = 0.37$). Similarly, for fecundity, the lack of significant difference between the observed and predicted pattern of independencies provided support for our model ($\chi^2 = 44.43$, $df = 38$, $P = 0.20$). Appendix Table A2 presents the independence tests for the two basis sets.

There are a number of key points to take from the birth traits model (Fig. 1b). Firstly, with the exception of $MaxT_t$ (the temperature period affecting birth date), all of the identified weather variables had a significant *direct* effect on the respective birth traits; this was as predicted from the models of weather variables only, but now also taking into account the other fixed effects. Warmer minimum temperatures in the period May to August ($MinT_t$) before conception were correlated with earlier birth dates, whereas higher wind speeds immediately prior to the rut were associated with delayed birth dates. Warmer springs immediately before birth ($MaxT2_t$) were correlated with greater birth mass. Finally, warmer maximum temperatures in May–July ($MaxT_{t+1}$) and minimum temperatures in May ($MinT_{t+1}$, around the time of birth) were associated with reduced first-year survival of calves, as was more rainfall between July and February in the first year of life.

The second point to note is that $MaxT_t$ and $MinT_t$ both significantly increased over time (Fig. 1b; see also Appendix Fig. A1.b for annual averages of temperature). These increases are relevant to changes in deer traits over time because $MinT_t$ had a direct effect on birth date, whereas $MaxT_t$ was associated with birth mass indirectly via its association with the second period in which temperature was relevant, $MaxT2_t$. Finally, the increasing population size had a direct negative effect on birth mass. Population size also indirectly affected birth date, birth mass, and juvenile survival via reproductive status and age, with increased population size positively (but weakly) correlated both with maternal age and with females being yeld rather than milk (Fig. 1b).

Our model of fecundity shows that increasing rainfall immediately prior to the rut had a direct negative effect on female fecundity (Fig. 2b). However, maximum temperature at the beginning of the rut was associated with fecundity only indirectly in the full path analysis: maternal age was apparently negatively associated with warmer temperatures, leading indirectly to a reduction in fecundity. In contrast to our model of birth traits, neither weather variable included in this model showed any evidence of a significant temporal trend (Fig. 2b). Increasing population size was directly associated with reduced fecundity; however, indirectly, via associated changes in maternal age and reproductive status, population size also had a small, positive effect on fecundity.

Observed and predicted temporal trends

Across the study period, average birth date advanced by 0.15 ± 0.05 days per year, mean $\pm$ SE (Fig. 3a); this change was significant as indicated by the 95% confidence intervals surrounding the observed change in birth date not overlapping zero (Fig. 4a). However, neither birth mass nor juvenile survival changed significantly over the study period: birth mass declined by only -0.002 ± 0.005 kg/yr, mean $\pm$ SE (Fig. 3b), and the log(odds) of juvenile survival changed by -0.002 ± 0.002, mean $\pm$ SE (Fig. 3c). For all three birth traits, the

←
a female being "yeld" (first-time mothers or no calf) rather than "milk" (with a live calf from the previous year); for sex, the effect is of the offspring being male rather than female. Subscript t refers to deer year, from 1 May in year t to 30 April in year $t + 1$. Nonsignificant paths ($P > 0.05$) shown as darker lines in panel (a) have been set as light gray lines in panel (b).

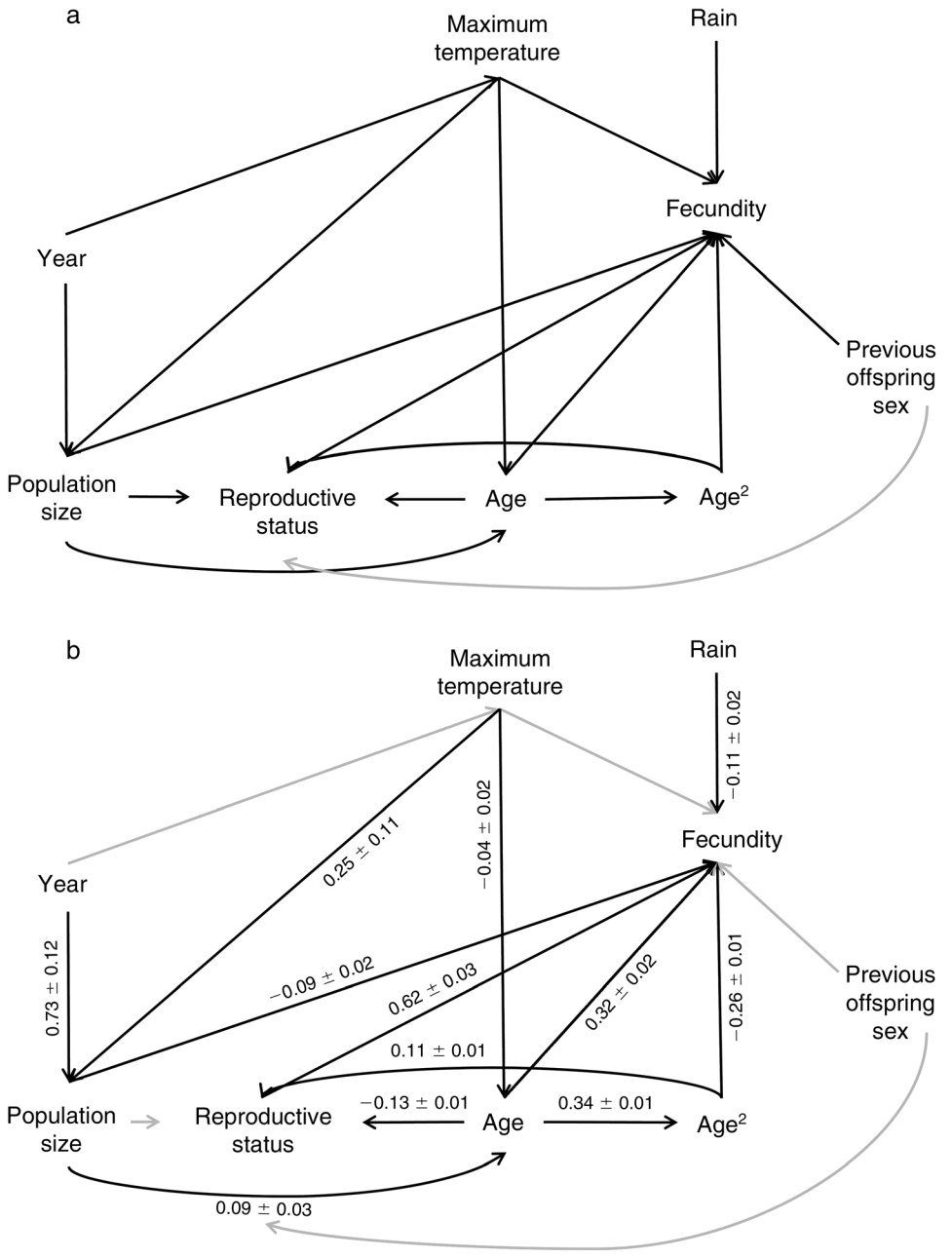

FIG. 2. (a) Hypothesized fecundity path model. See *Methods* for definitions of weather variables and for explanation of hypothesized relationships. (b) Fecundity path model with standardized coefficients (β) given for significant paths; see Fig. 1b for further details. Nonsignificant paths ($P > 0.05$) shown as darker lines in panel (a) have been set as light gray lines in panel (b).

standardized observed temporal change over the study period fell within the 95% confidence interval of the standardized change predicted by our model (Fig. 4a–c).

Consideration of the different pathways by which traits were affected by both weather and demography illustrates how the apparent stasis in birth mass and juvenile survival may be due to multiple effects cancelling each other out. For example, when the paths leading from year to birth mass via all of the weather variables are summed (the paths in the upper half of Fig. 1a), we would predict a net increase of 0.056 (standardized data, 95% CI = 0.055–0.058) in mean birth mass; in contrast, summing the paths acting via population size would predict an almost exactly equivalent net decrease in mean birth mass of −0.051 (standardized data, 95% CI = −0.054 to −0.048). The final result is the observed stasis in mean birth mass. For juvenile survival, the indirect effects of weather via birth date and birth mass

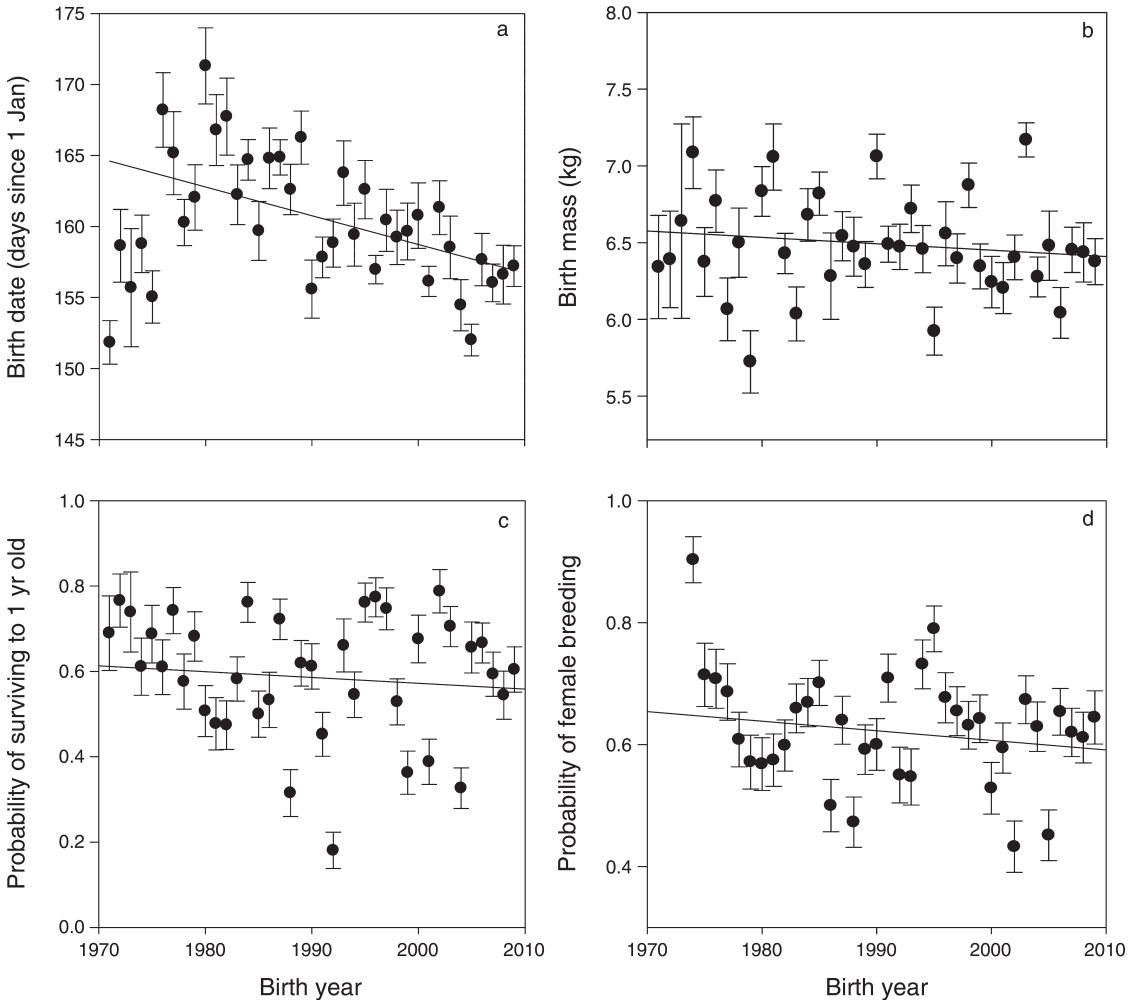

FIG. 3. Observed temporal changes in (a) birth date, (b) birth mass, (c) juvenile survival (all 1971–2009), and (d) female fecundity (1974–2009), using unstandardized values (mean ± SE). The regression lines shown are fitted through all data points.

were positive (0.020, standardized data, 95% CI = 0.009–0.036), but the direct effect of weather on juvenile survival was negative (−0.024, standardized data, 95% CI = −0.057 to −0.002). Therefore, the overall effect of weather on juvenile survival was small, as was the sum of paths which acted via population size (−0.011, standardized data, 95% CI = −0.027–0.002); combined, these effects predict no change in juvenile survival.

There was a trend toward a decrease in observed fecundity over time, but this was not significant: the log(odds) of a female breeding changed by only −0.002 ± 0.001/yr (Fig. 3d). However, the path analysis model predicted a significant decline in fecundity over the study period (mean standardized prediction = −0.070; all 1000 estimated coefficients were negative; Fig. 5). Nevertheless, despite these different conclusions with regard to statistical significance, the observed standardized change fell within the 95% confidence interval of the (standardized) predictions (Fig. 5).

DISCUSSION

In this study, we used path analysis to test whether changes or stasis over nearly 40 years in four reproductive traits—offspring birth date, offspring birth mass, offspring juvenile survival, and female fecundity—in red deer could be predicted from combined effects of changing climate and rising population density. Doing so provided an explanation as to why no apparent effects of climate change were observed on components of fitness, despite the substantial changes in phenology observed in the same population (Moyes et al. 2011): temporal stasis in average trait values could, at least in part, be explained by antagonistic roles of direct and indirect effects of changing climate and increasing population density. The utility of the path analyses that we have conducted, and their value in understanding trait change or stasis, are demonstrated by the finding that, for each trait, the change predicted by the path analysis was in agreement with the observed change or stasis. Combining an understanding of climatic effects,

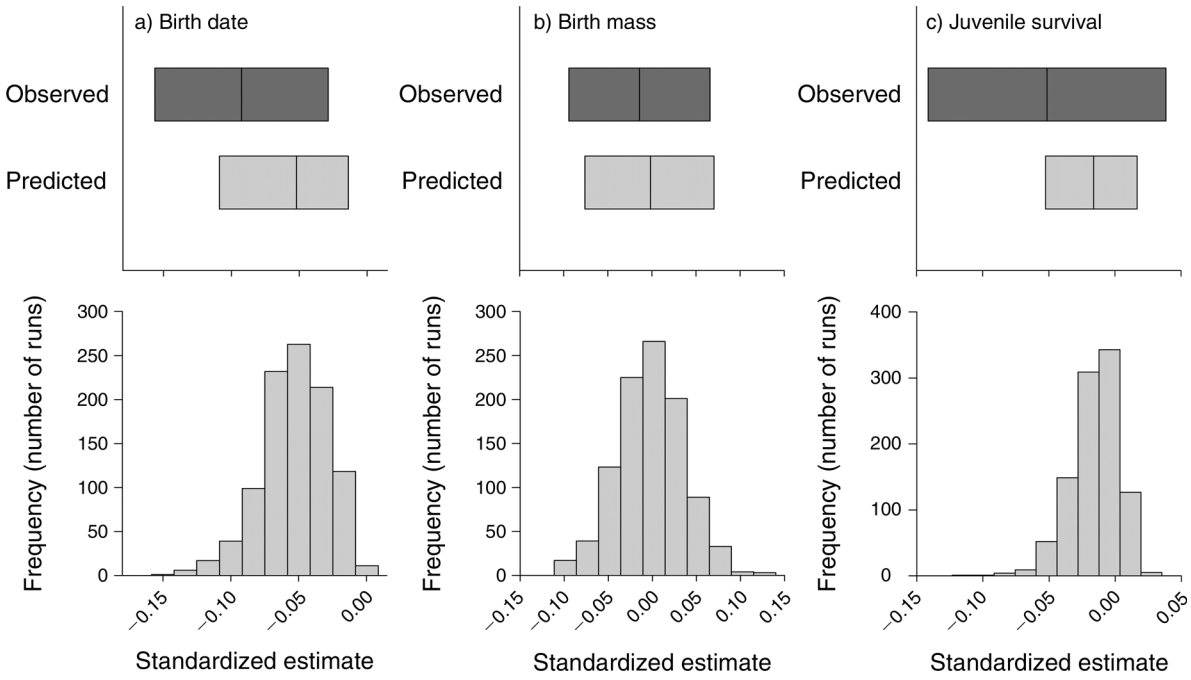

FIG. 4. Observed and predicted standardized rates of change for (a) birth date, (b) birth mass, and (c) juvenile survival, with predictions calculated using the distributions of each relevant path coefficient from Fig. 1b. In the upper panels, the upper box (dark gray) indicates the mean and 95% confidence intervals of the observed temporal trend in each trait. The lower box (light gray) indicates the mean and 95% confidence intervals of the distribution of predictions. In the lower panels, the distribution of predictions shown for each trait is for 1000 runs of the prediction analysis, on each run sampling a new value from the distributions of each of the path coefficients (see *Methods*).

effects of population size, and maternal attributes has therefore allowed us to make predictions that are in accordance with the observed patterns in key reproductive traits.

The associations between our focal traits and weather variables in particular time windows were broadly, although not entirely, in accordance with previous findings from the long-term study of red deer on Rum: warmer temperatures were associated with earlier birth dates and heavier birth mass, whereas higher rainfall was associated with reduced juvenile survival and reduced female fecundity (Albon et al. 1987, Coulson et al. 1998, 2003, Kruuk et al. 1999, Nussey et al. 2005*a*, *b*, Sims et al. 2007, Moyes et al. 2011, Walling et al. 2011). However, we also found new evidence of warmer temperatures in spring/summer being directly associated with reduced juvenile survival in the first year of life, of effects of wind during the rut on birth date, and of adverse associations of increasing population size with birth mass. We present a detailed discussion of these various associations and possible explanations for differences from studies from earlier years in the Appendix. Here, we discuss the more general implications of the information gained from the path analysis approach.

We used a sliding-window approach to identify critical windows of weather affecting trait expression. This approach has been widely used across a range of study systems (e.g., Estrella et al. 2007, Brommer et al. 2008, Husby et al. 2010, Phillimore et al. 2013), and provides an easily implemented and easily interpreted means of assessing the impact of climate at different time points. However, it also clearly has some limitations, firstly because it assumes that all days within a critical window exert equal influence on the trait, and secondly because the arbitrary nature of the cutoff points used (for example, the start and end of a week, as used here) may not be biologically realistic (Sims et al. 2007, van de Pol and Cockburn 2011). Methods have been developed that allow the former issue to be addressed, for example allowing days to increase in their influence as they near the date of trait expression (Gienapp et al. 2005, van de Pol and Cockburn 2011). However, although some of these allow for a time lag between the window and expression of the trait (van de Pol and Cockburn 2011), to our knowledge, no study has yet demonstrated their application when the critical window occurs several months before the trait is expressed, as is the case for traits such as parturition date as considered here. The second problem, that the cutoff points of the critical windows are arbitrary, is relevant to this study, and is highlighted by the fact that a number of the critical windows that we have identified are very short (at the most extreme, the critical window of rainfall identified for fecundity was only one week long). Although these short windows were statistically

the "best" in terms of having highest support (and in the case of the rainfall effects on fecundity, there was a difference of more than 2 between the AIC of a model containing that window and the next best model; Fig. A5), it seems unlikely, biologically, that the true critical window is as precise as that identified. Therefore the exact dates of the windows identified should be assumed to indicate statistical support for the finding that, in the average year, the value of the weather variable in the identified critical window is significantly associated with trait expression. It should not be taken to imply that weather outside of the identified critical window (which may well be correlated) is entirely unimportant.

A key paradox noted by previous work on this red deer population (Moyes et al. 2011) is that although birth dates had advanced over recent decades, there is no evidence of change in either offspring birth mass or first-year survival, despite known associations between birth date, birth mass, and first-year survival. The apparent stasis is unlikely to be due to a lack of statistical power to detect any change, given the large sample sizes and the fact that we were able to detect change in birth date (and in the other phenological traits reported in Moyes et al. 2011). However, the results from our path analyses were able to resolve this paradox. When direct and indirect effects of weather, population size, maternal attributes, and upstream traits (i.e., birth date) were considered simultaneously, the influence of each on birth mass and juvenile survival counteracted one another such that no net change was predicted. Consideration of the combined effects of the different mechanisms causing changes in birth mass and juvenile survival over time was therefore necessary to explain the observed stasis. As has been noted elsewhere, identification of the potential effects of population demography, at both the individual and population level, is therefore critical for understanding change or stasis in average trait values, because such changes may reinforce or counteract trait change driven by climatic mechanisms (van de Pol et al. 2012).

In addition to the offspring traits of birth date, birth mass, and juvenile survival, we also tested for possible changes in female fecundity. Although there has been no significant decline in fecundity over the study period, there is a trend toward this. Our path model indicates that fecundity was density dependent, and that the decline can be explained by the increase in population size over the study period. Should the population size continue to increase, there is clearly potential for future declines in fecundity; note also that fecundity was not affected by any weather variables that are changing over time, so there is no apparent weather effect to counter the density-dependent effects. Future changes in fecundity will therefore be largely dependent on whether the population continues to grow in size. It has been well documented that the cessation of culling at the start of the study period resulted in an increase in the number of adult females living in the study area (alongside other demographic effects on mortality and sexual segregation; Coulson et al. 2004). However, the increase in population size since 1980 (albeit at a lower rate; Fig. A1a) has received less attention. Given that our findings suggest that juvenile survival and female fecundity are not increasing, the increase in the number of females is presumably attributable to adult female survival. Indeed, Albon et al. (2000) found that the contribution of adult winter survival to population growth had increased relative to the contribution of birth rate during the 1980s and 1990s. The effect of climate on adult survival is not known in this population: although adult female survival may generally show less year-to-year variation than other fitness components in large herbivores (Gaillard et al. 2000), effects of climate on adult overwinter survival have been shown for other ungulate species (Forchhammer et al. 1998, Milner et al. 1999). Further work is therefore needed to identify the effects of climate change on female adult survival rates in this population in order to understand the factors determining population growth.

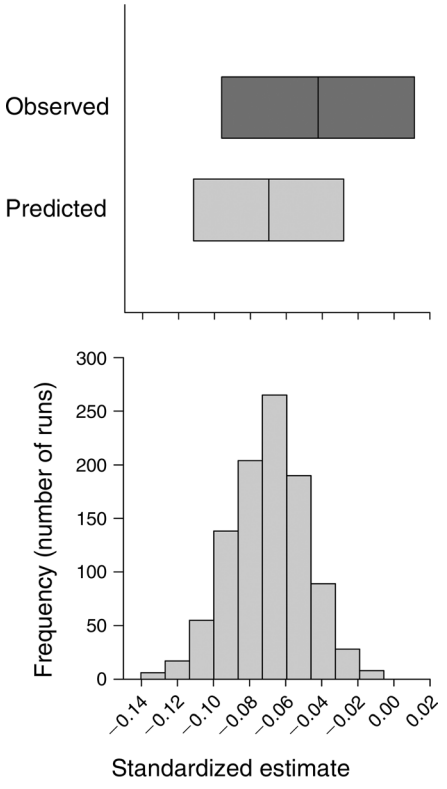

FIG. 5. Observed and predicted standardized rates of change for fecundity, with predictions calculated using the distributions of each relevant path coefficient from Fig. 2b. In the lower panel, the distribution of predictions shown is for 1000 runs of the prediction analysis, on each run sampling a new value from the distributions of each of the path coefficients (see *Methods*). In the upper panel, the upper box (dark gray) indicates the mean and 95% confidence intervals of the observed temporal trend. The lower box (light gray) indicates the mean and 95% confidence intervals of the distribution of predictions.

In comparison to our study population, the majority of red deer populations across Scotland are managed at relatively lower population densities. Our models suggest that in the absence of strong density-dependent effects, changes in climate might potentially drive an increase in the birth mass of calves. In contrast, changes in juvenile survival are still predicted to be small due to the multiple counteracting direct and indirect climatic effects (see Appendix). However the ability to make such predictions clearly relies on the assumption that the timing and magnitude of the effect of climate is consistent across different levels of management. Various reasons exist as to why such an assumption may not be justified: for example, under lower densities, the timing of when environmental stress affects juvenile survival may be delayed, and studies of ungulate species elsewhere, including red deer, have reported differences between populations in responses to climate (e.g., Pettorelli et al. 2007, Martinez-Jauregui et al. 2009). Therefore, it would be highly useful to determine whether the critical windows of climate effects on maternal reproductive traits are consistent between populations.

For ungulates, although physiological condition during winter may depend on direct effects of weather, effects of weather during spring and summer are especially likely to be mediated through their effects on vegetation (e.g., Pettorelli et al. 2005, Mysterud et al. 2008). Determining associations between weather and plant productivity is itself a major challenge: for example, it is possible for spring/summer temperatures to have entirely contrasting associations with remotely sensed measure of vegetation productivity (e.g., the normalized difference vegetation index, or NDVI) in different populations (Pettorelli et al. 2007, Mysterud et al. 2008), and also for associations between NDVI and ungulate mass to vary between populations (e.g., Pettorelli et al. 2006, Martinez-Jauregui et al. 2009). Nevertheless, identifying rates of change in the plant growing season will be important because one of the key concerns surrounding the ability of animal populations to respond to climate change is the potential for mismatch between trophic levels in the rate of response (Thackeray et al. 2010, Reed et al. 2013). For example, in herbivores, the peak of grass abundance may advance faster than the rate of reproductive traits such as birth date. Such a mismatch has been documented in caribou, resulting in a reduction in offspring survival and production (Post and Forchhammer 2008), and roe deer have also been shown to be unable to adjust the timing of birth to changes in spring temperature, resulting in a marked decrease in early fawn survival (Gaillard et al. 2013). For the Rum red deer study, the next stage for our analyses will be to incorporate measures of vegetation growth and resource availability, as doing so should provide useful insights into the mechanisms driving the associations reported here. Recent analyses of measures of plant standing crop, offtake, and productivity indicate that the vegetation is most dependent on temperatures in late winter and early spring, presumably because high temperatures in a given year can advance the start of the growing season, which, in turn, can affect plant productivity for the year as a whole (A. I. R. Bento, J. M. Pemberton, L. E. B. Kruuk, T. H. Clutton-Brock, and M. J. Crawley, *unpublished manuscript*).

In summary, in contrast to studies reporting temporal trends in ungulate life history traits, in our study population of red deer, changes in climate do not appear to be generating changes in juvenile fitness. Here we have shown that this apparent resilience of red deer to changes in climate is probably due to (1) concurrent changes in population density; (2) an additional, positive, direct effect of spring temperature on birth mass acting antagonistically to the effects of changes in climate on birth dates; and (3) antagonism between the effects of birth date and birth mass on juvenile survival and the negative effects of warm spring temperatures. Our analyses illustrate how a lack of an apparent trend in association with changing weather is not necessarily indicative of a population being insensitive to climate change. They also highlight the need to jointly consider multiple aspects of climatic and demographic variation if we hope to fully understand the consequences of changes in phenology for individual fitness.

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Literature Cited

Albon, S. D., T. H. Clutton-Brock, and F. E. Guinness. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. Journal of Animal Ecology 56:69–81.

Albon, S. D., T. N. Coulson, D. Brown, F. E. Guinness, J. M. Pemberton, and T. H. Clutton-Brock. 2000. Temporal changes in key factors and key age groups influencing the population dynamics of female red deer. Journal of Animal Ecology 69:1099–1110.

Albon, S. D., F. E. Guinness, and T. H. Clutton-Brock. 1983. The influence of climatic variation on the birth weights of red deer (*Cervus elaphus*). Journal of Zoology 200:295–298.

Barnett, C., J. Hossell, M. Perry, C. Procter, and G. Hughes. 2006. Patterns of climate change across Scotland: Technical Report. Scotland and Northern Ireland Forum for Environmental Research Project CC03:102.

Bento, A. I. R. 2012. Climate variation, plant productivity, herbivore performance and population dynamics. Dissertation. Imperial College, London, UK.

Berteaux, D., and N. C. Stenseth. 2006. Measuring, understanding and projecting the effects of large-scale climatic variability on mammals. Climate Research 32:95–97.

Brommer, J. E., K. Rattiste, and A. J. Wilson. 2008. Exploring plasticity in the wild: Laying date–temperature reaction norms in the common gull *Larus canus*. Proceedings of the Royal Society B 275:687–693.

Burthe, S., A. Butler, K. R. Searle, S. J. G. Hall, S. J. Thackeray, and S. Wanless. 2011. Demographic consequences of increased winter births in a large aseasonally breeding mammal (*Bos taurus*) in response to climate change. Journal of Animal Ecology 80:1134–1144.

Cahill, A. E., et al. 2013. How does climate change cause extinction? Proceedings of the Royal Society B 280:20121890.

Catchpole, E. A., Y. Fan, B. J. T. Morgan, T. H. Clutton-Brock, and T. Coulson. 2004. Sexual dimorphism, survival and dispersal in red deer. Journal of Agricultural, Biological and Environmental Statistics 9:1–26.

Charmantier, A., R. H. McCleery, L. R. Cole, C. Perrins, L. E. B. Kruuk, and B. C. Sheldon. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320:800–803.

Chevin, L.-M., R. Lande, and G. M. Mace. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. PLoS Biology 8:e1000357.

Clements, M. N., T. H. Clutton-Brock, S. D. Albon, J. M. Pemberton, and L. E. B. Kruuk. 2011. Gestation length variation in a wild ungulate. Functional Ecology 25:691–703.

Clutton-Brock, T., F. Guinness, and S. Albon. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois, USA.

Coulson, T., S. Albon, J. Slate, and J. M. Pemberton. 1999. Microsatellite loci reveal sex dependent responses to inbreeding and outbreeding in red deer calves. Evolution 53:1951–1960.

Coulson, T., F. Guinness, J. Pemberton, and T. Clutton-Brock. 2004. The demographic consequences of releasing a population of red deer from culling. Ecology 85:411–422.

Coulson, T., L. E. B. Kruuk, G. Tavecchia, J. M. Pemberton, and T. H. Clutton-Brock. 2003. Estimating selection on neonatal traits in red deer using elasticity path analysis. Evolution 57:2879–2892.

Coulson, T., E. Milner–Gulland, and T. Clutton–Brock. 2000. The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. Proceedings of the Royal Society B 267: 1771–1779.

Coulson, T. N., S. D. Albon, J. M. Pemberton, J. Slate, F. E. Guinness, and T. H. Clutton-Brock. 1998. Genotype by environment interactions in winter survival in red deer. Journal of Animal Ecology 67:434–445.

Dickinson, R. 1986. The climate system and modelling of future climate. Pages 207–270 *in* B. Bolin, B. R. Döös, J. Jäger, and R. A. Warrick, editors. The greenhouse effect, climate change, and ecosystems. Wiley, Chichester, UK.

Estrella, N., T. H. Sparks, and A. Menzel. 2007. Trends and temperature response in the phenology of crops in Germany. Global Change Biology 13:1737–1747.

Forchhammer, M., and E. Post. 2004. Using large-scale climate indices in climate change ecology studies. Population Ecology 46:1–12.

Forchhammer, M. C., N. C. Stenseth, E. Post, and R. Landvatn. 1998. Population dynamics of Norwegian red deer: density-dependence and climatic variation. Proceedings of the Royal Society B 265:341–350.

Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gaillard, J. M., A. J. M. Hewison, F. Klein, F. Plard, M. Douhard, R. Davison, and C. Bonenfant. 2013. How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. Ecology Letters 16:48–57.

Geiger, D., T. Verma, and J. Pearl. 1990. Identifying independence in Bayesian networks. Networks 20:507–534.

Gienapp, P., L. Hemerik, and M. E. Visser. 2005. A new statistical tool to predict phenology under climate change scenarios. Global Change Biology 11:600–606.

Gienapp, P., M. Lof, T. E. Reed, J. McNamara, S. Verhulst, and M. E. Visser. 2013. Predicting demographically sustainable rates of adaptation: can great tit breeding time keep pace with climate change? Philosophical Transactions of the Royal Society B 368:20120289.

Guinness, F., G. A. Lincoln, and R. V. Short. 1971. The reproductive cycle of the female red deer, *Cervus elaphus* L. Journal of Reproduction and Fertility 27:427–438.

Husby, A., D. H. Nussey, M. E. Visser, A. J. Wilson, B. C. Sheldon, and L. E. B. Kruuk. 2010. Contrasting patterns of phenotypic plasticity in reproductive traits in two great tit (*Parus major*) populations. Evolution 64:2221–2237.

Karl, T. R., and K. E. Trenberth. 2003. Modern global climate change. Science 302:1719–1723.

Kruuk, L. E. B., T. H. Clutton-Brock, S. D. Albon, J. M. Pemberton, and F. E. Guinness. 1999. Population density affects sex ratio variation in red deer. Nature 399:459–461.

Lane, J. E., L. E. B. Kruuk, A. Charmantier, J. O. Murie, and F. S. Dobson. 2012. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. Nature 489:554–557.

Martinez-Jauregui, M., A. San Miguel-Ayanz, A. Mysterud, C. Rodríguez-Vigal, T. H. Clutton-Brock, R. Langvatn, and T. N. Coulson. 2009. Are local weather, NDVI and NAO consistent determinants of red deer weight across three contrasting European countries? Global Change Biology 15: 1727–1738.

Milner, J. M., D. A. Elston, and S. D. Albon. 1999. Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. Journal of Animal Ecology 68:1235–1247.

Moritz, C., and R. Agudo. 2013. The future of species under climate change: resilience or decline? Science 341:504–508.

Moyes, K., D. H. Nussey, M. N. Clements, F. E. Guinness, A. Morris, S. Morris, J. M. Pemberton, L. E. B. Kruuk, and T. H. Clutton-Brock. 2011. Advancing breeding phenology in response to environmental change in a wild red deer population. Global Change Biology 17:2455–2469.

Mysterud, A., N. G. Yoccoz, R. Langvatn, N. Pettorelli, and N. C. Stenseth. 2008. Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. Philosophical Transactions of the Royal Society B 363:2359–2368.

Nussey, D. H., T. H. Clutton-Brock, S. D. Albon, J. Pemberton, and L. E. B. Kruuk. 2005*a*. Constraints on plastic responses to climate variation in red deer. Biology Letters 1:457–460.

Nussey, D. H., T. H. Clutton-Brock, D. A. Elston, S. D. Albon, and L. E. B. Kruuk. 2005*b*. Phenotypic plasticity in a maternal trait in red deer. Journal of Animal Ecology 74: 387–396.

Nussey, D. H., L. E. B. Kruuk, A. Morris, M. N. Clements, J. M. Pemberton, and T. H. Clutton-Brock. 2009. Inter- and intrasexual variation in aging patterns across reproductive traits in a wild red deer population. American Naturalist 174: 342–357.

Ottersen, G., B. Planque, A. Belgrano, E. Post, P. Reid, and N. Stenseth. 2001. Ecological effects of the North Atlantic Oscillation. Oecologia 128:1–14.

Ozgul, A., D. Z. Childs, M. K. Oli, K. B. Armitage, D. T. Blumstein, L. E. Olson, S. Tuljapurkar, and T. Coulson. 2010. Coupled dynamics of body mass and population

growth in response to environmental change. Nature 466: 482–485.
Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669.
Pettorelli, N., J. M. Gaillard, A. Mysterud, P. Duncan, N. C. Stenseth, D. Delorme, G. Van Laere, C. Toigo, and F. Klein. 2006. Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. Oikos 112:565–572.
Pettorelli, N., F. Pelletier, A. von Hardenberg, M. Festa-Bianchet, and S. D. Cote. 2007. Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology 88:381–390.
Pettorelli, N., R. B. Weladji, O. Holand, A. Mysterud, H. Breie, and N. C. Stenseth. 2005. The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. Biology Letters 1: 24–26.
Phillimore, A. B., K. Proios, N. O'Mahony, R. Bernard, A. M. Lord, S. Atkinson, and R. J. Smithers. 2013. Inferring local processes from macro-scale phenological pattern: a comparison of two methods. Journal of Ecology 101:774–783.
Post, E., and M. C. Forchhammer. 2008. Climate change reduces reproductive success of an arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society B 363:2367–2373.
Post, E., and N. C. Stenseth. 1999. Climatic variability, plant phenology and northern ungulates. Ecology 80:1322–1339.
R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Réale, D., A. G. McAdam, S. Boutin, and D. Berteaux. 2003. Genetic and plastic responses of a northern mammal to climate change. Proceedings of the Royal Society B 270:591–596.
Reed, T. E., S. Jenouvrier, and M. E. Visser. 2013. Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. Journal of Animal Ecology 82:131–144.
Sæther, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology and Evolution 12:143–149.
Scottish Natural Heritage. 2010. Managing Scotland's deer. Scottish Natural Heritage, Battleby, Redgorton, Perth, Scotland. http://www.snh.gov.uk/docs/A415809.pdf
Shipley, B. 2000*a*. Cause and correlation in biology. Cambridge University Press, Cambridge, UK.
Shipley, B. 2000*b*. A new inferential test for path models based on directed acyclic graphs. Structural Equation Modeling 7: 206–218.
Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368.
Sims, M., D. A. Elston, A. Larkham, D. H. Nussey, and S. D. Albon. 2007. Identifying when weather influences life-history traits of grazing herbivores. Journal of Animal Ecology 76: 761–770.
Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller. 2007. Intergovernmental Panel on Climate Change. The physical science basis. Contribution of Working Group 1 to the Fourth Assessment Report of the IPCC. Cambridge University Press, Cambridge, UK.
Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292–1296.
Thackeray, S. J., et al. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Global Change Biology 16:3304–3313.
Thomas, D. W., B. Shipley, J. Blondel, P. Perret, A. Simon, and M. M. Lambrechts. 2007. Common paths link food abundance and ectoparasite loads to physiological performance and recruitment in nestling blue tits. Functional Ecology 21:947–955.
Torres-Porras, J., J. Carranza, and J. Pérez-González. 2009. Combined effects of drought and density on body and antler size of male Iberian red deer *Cervus elaphus hispanicus*: climate change implications. Wildlife Biology 15:213–221.
van de Pol, M., et al. 2013. Problems with using large-scale oceanic climate indices to compare climatic sensitivities across populations and species. Ecography 36:249–255.
van de Pol, M., and A. Cockburn. 2011. Identifying the critical climatic time window that affects trait expression. American Naturalist 177:698–707.
van de Pol, M., H. L. Osmond, and A. Cockburn. 2012. Fluctuations in population composition dampen the impact of phenotypic plasticity on trait dynamics in superb fairy-wrens. Journal of Animal Ecology. 81:411–422.
Verma, T. 1988. Causal networks: Semantics and expressiveness. Pages 352–359 *in* Proceedings of the Fourth Workshop on Uncertainty in Artificial Intelligence. Morgan Kaufmann, Mountain View, California, USA.
Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society B: Biological Sciences 275:649–659.
Visser, M. E., et al. 2003. Variable responses to large-scale climate change in European *Parus* populations. Proceedings of the Royal Society B 270:367–372.
Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society B 272:2561–2569.
Visser, M. E., C. Both, and M. M. Lambrechts. 2004. Global climate change leads to mistimed avian reproduction. Pages 89–110 *in* A. P. Moller, W. Fiedler, and P. Berthold, editors. Advances in Ecological Research. Volume 35: Birds and climate change. Academic Press, New York, New York, USA.
Visser, M. E., A. J. van Noordwijk, J. M. Tinbergen, and C. M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proceedings of the Royal Society B 265:1867–1870.
Walling, C., D. Nussey, A. Morris, T. Clutton-Brock, L. Kruuk, and J. Pemberton. 2011. Inbreeding depression in red deer calves. BMC Evolutionary Biology 11:318.
Weladji, R. B., and O. Holand. 2003. Global climate change and reindeer: effects of winter weather on the autumn weight and growth of calves. Oecologia 136:317–323.

Supplemental Material

Ecological Archives

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